CLASSIFICATION OF THE RIPARIAN VEGETATION ALONG A 6-KM REACH OF THE ANIMAS RIVER, SOUTHWESTERN COLORADO

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ABSTRACT.—Riparian ecosystems are important components of landscapes, particularly because of their role in biodiversity. A first step in using a "coarse-filter" approach to riparian biodiversity conservation is to determine the kinds of riparian ecosystems. These ecosystems vary substantially in plant species composition along a single river reach, as well as between rivers, and yet the river-reach scale has received little attention. We sampled the vascular plant composition of 67 contiguous patches of riparian vegetation along a reach of the Animas River, in southwestern Colorado's San Juan Mountains, that is relatively undisturbed by human land uses. Using cluster analysis and detrended correspondence analysis, we identified eight riparian community types along the reach. Using a new technique, we combined overstory size-class data and understory cover data to identify community types. The eight community types, which are in part the products of past floods, are spatially arranged along the reach in relation to variation in valley morphology, tributary location, and geomorphic landforms. These eight community types do not necessarily represent successional stages of a single potential vegetation type. This study at the river-reach scale suggests that sampling and analysis, as well as conservation, may need to be tuned to the scale of patchiness produced by flood disturbances in the riverine landscape, since vegetation varies significantly at this scale.

Key words: riparian vegetation, Rocky Mountains, Colorado, multivariate analysis.

Riparian vegetation provides several important functions in landscapes, and riparian communities have thus been a focus for conservation. Riparian vegetation contributes to water quality, stream bank stability, and healthy fish habitat (Johnson et al. 1985, Malanson 1993). Riparian vegetation also provides cover and forage for wildlife that is particularly important in the arid portions of North America (Knopf 1985). The idea of a "coarse-filter" approach to biodiversity conservation is that by preserving viable communities, associated species also will be preserved (Hunter 1991, O'Connell and Noss 1992).

Classification of vegetation communities is an essential first step in implementing this coarse-filter conservation approach, but classification of riparian vegetation in the Rocky Mountains is incomplete. The montane and subalpine riparian zones of Colorado's western slope have been classified (Baker 1989). Riparian community type classifications for U.S. Forest Service lands in Utah and parts of Idaho and Wyoming are available (Mutz and

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Graham 1982, Youngblood et al. 1985a, 1985b, Padgett et al. 1989). A riparian-wetland classification and key were produced for Montana (Hansen et al. 1991), and other classifications are available for small parts of the Rocky Mountains (Mutz and Graham 1982, Cooper and Cottrell 1990).

Methods of riparian vegetation classification vary with the researcher and project goals. The U.S. Forest Service classifies forest ecosystems into "habitat types" based on potential climax vegetation (Daubenmire 1952, Pfister and Arno 1980). Climax vegetation represents the stable, self-perpetuating community predicted on the basis of climate, topography, and soils in the absence of disturbance. Often, however, riparian vegetation never reaches climax due to frequent floods (Campbell and Green 1968). Therefore, some researchers classify vegetation into "community types" according to existing structure and composition without reference to successional stage following disturbance. This approach, however, is not concerned with whether vegetation consists primarily of native or exotic species or has been disturbed by human land uses (e.g., Youngblood et al. 1985b, Padgett et al. 1989). Another classification approach (1) recognizes that climax vegetation is seldom reached due to natural disturbances, but focuses on the more mature successional stages; and (2) emphasizes that classification of "natural vegetation," vegetation that is as free as possible of exotic species and the effects of human land uses, provides essential information for effective biodiversity conservation (Baker 1989). Vegetation types classified using either a habitat type approach or Baker's approach are referred to as "associations."

Even if there is only one association along a river reach, there may be several community types. Riparian community types along a river reach comprise a complex which Winward and Padgett (1989) name on the basis of the most prominent community type plus geographical features describing where it occurs. This spatially complex mosaic of community types creates difficulties for classification, but the diversity of communities is an important component of biodiversity (Hunter 1991).

An additional problem is that classification may use only overstory species, or it may be based on the entire flora. Classification traditionally uses one technique or a combination of techniques including subjective grouping, evaluating and sorting of stand tables, cluster analysis, or ordination (Whittaker 1962, Gauch 1982). However, the dominance of the overstory in forests may skew mathematical analyses that use the entire flora (Padgett et al. 1989). In northern regions, where the understory flora often is more sensitive to environmental variation than is the overstory (Whittaker 1962), quantitative techniques that give equal weight to the understory and overstory may not be ideal.

Along the Animas River in southwestern Colorado's San Juan Mountains, we investigated variation in plant species composition of contiguous patches of riparian vegetation. We classified riparian vegetation along a 6-km reach using both understory and overstory vegetation. Goals of this paper are to identify community types found along the river reach, to describe the community types in relation to their environment, and to explain a new approach to balance the use of both overstory and understory vegetation data in quantitative classification. This approach, we suggest, may lead to community classifications more useful for conservation and management.

STUDY AREA

The Animas River starts in the San Juan Mountains of southwestern Colorado and flows south to the San Juan River in New Mexico. The study area is approximately 40 km northeast of Durango in LaPlata County (Fig. 1), along a continuous 6-km reach of the Animas River between 2430 and 2550 m in elevation. This is one of the least disturbed montane river reaches in western Colorado (Baker 1990). A narrow-gauge railroad track and a wilderness access trail occur along the reach, but the reach has probably never been grazed by cattle or sheep. There are some silver and gold mines upstream.

The Animas is an unregulated gravelbed river with a mean annual peak flow of 145 m^3s^{-1}. Within the study reach the river has a mean gradient of 0.0193, a mean channel width of 34.3 m, and a mean channel depth of 3.6 m. The river is entrenched in a deep canyon surrounded by the Needle Mountains. The valley, varying in width from less than 100 m to about 400 m, is lined with alluvial deposits formed from Precambrian granites in the north and south

Community Types

Populus angustifolia / Alnus incana

Populus angustifolia / Agrostis scabra

Populus angustifolia - Pseudotsuga menziesii / Pyrola asarifolia

Picea pungens - Populus angustifolia / Antennaria parvifolia

Picea pungens / Alnus incana / Equisetum arvense

Picea pungens - Populus tremuloides / Mahonia repens

Pseudotsuga menziesii / Acer glabrum
   / Pyrola asarifolia

Populus tremuloides - Pseudotsuga menziesii
   / Bromus ciliatus

Not sampled

Animas River
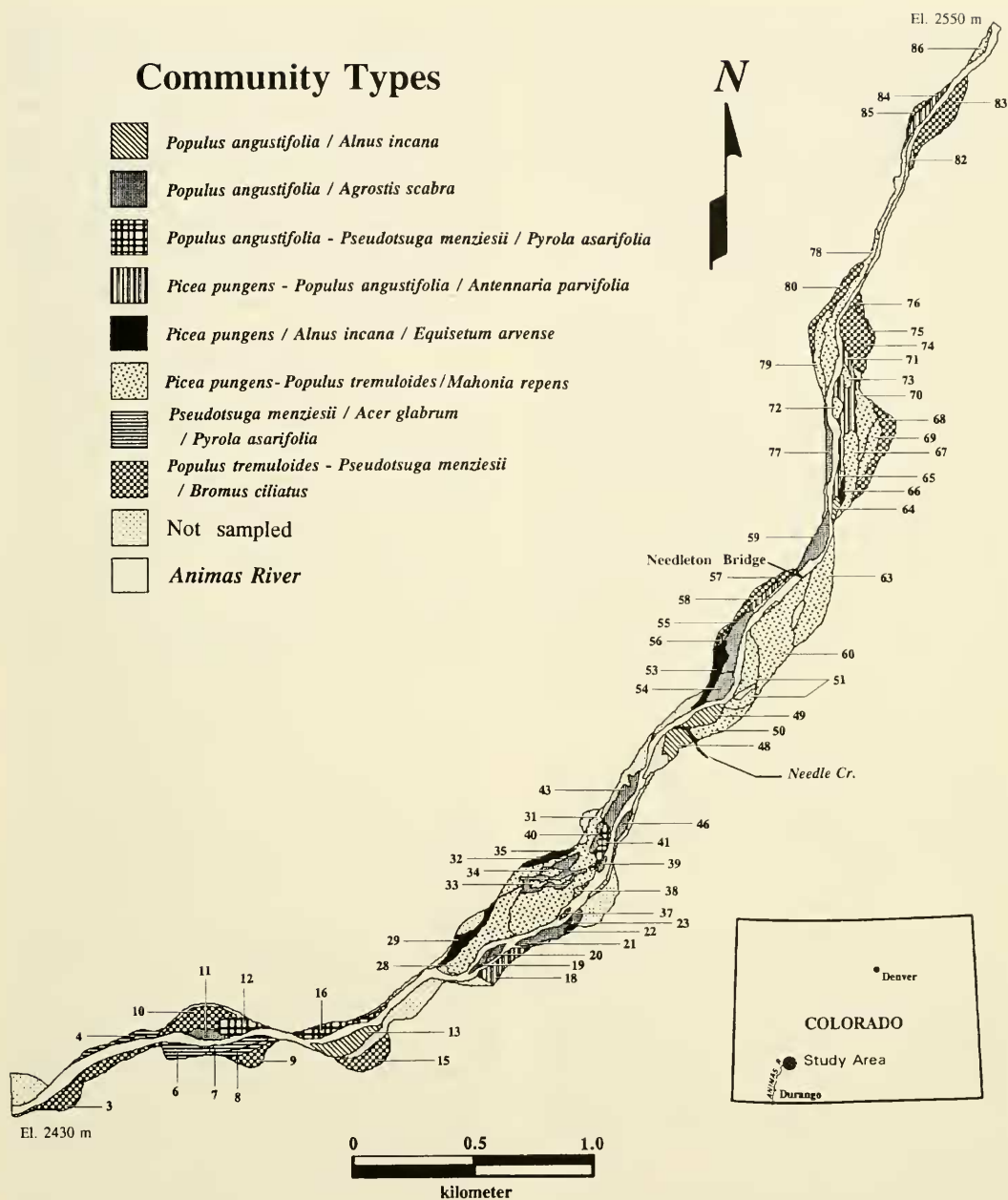
Fig. 1. Animas River study area and its location in Colorado. Patches are shaded according to their community type and numbered for identification.

sections of the study area and from Precambrian gneiss and schist in the central section of the study area (Osterwald 1989).

METHODS

Previous work on the study reach focused on the structure of riparian tree populations in rela-

tion to floods and climatic fluctuations (Baker 1988, 1990). Baker (1988) identified 57 vegetation patches having distinct boundaries recognizable on aerial photographs and on the ground. This patchiness is largely the result of tree regeneration after past floods (Baker 1990). In the field we refined the boundaries of some of the 57 patches and identified new patches

for a total of 67 patches available for sampling. Patches were mapped on aerial photographs in the field, then digitized and rectified using the GRASS geographic information system (USA-CERL 1991). A final map of patch locations and vegetation (Fig. 1) was produced with ATLAS Draw (Strategic Mapping 1991).

Vegetation Sampling and Environmental Data

Within each of the 67 patches, one 20 × 50-m plot (0.1 ha) was subjectively placed parallel to the river to obtain a representative sample of herbaceous and woody vegetation. Methods of herbaceous vegetation sampling followed Peet (1981). Percent cover of each vascular plant species (except trees) present was estimated, during mid-growing season, in 25 contiguous 0.5 × 2-m quadrats along the 50-m center line of each plot. Percent cover of 0–10% was estimated to the nearest 1%; percent cover of 10–100% was estimated to the nearest 5%. Species located during a survey of the plot, but not found in the quadrats, were assigned 0.1% cover. Nomenclature follows Kartesz and Kartesz (1980).

Baker (1988) collected data on diameter-at-breast-height (dbh) size classes of tree species in his original 57 stands. We added to this data set by tallying trees (>2.5 cm dbh in 10-cm classes), saplings (<2.5 cm dbh and >1 m tall), and seedlings (<2.5 cm dbh and <1 m tall) of each species in plots of the 10 additional patches as Baker had done. Increment cores were extracted from the bases of 5–15 of the largest trees in each patch for estimating patch age. Ages of the largest trees tend to be similar, reflecting a common origin following floods (Baker 1990). Each patch was assigned to a 10-year age class according to the maximum age of the 5–15 cored trees. Age zero is A.D. 1990.

A set of environmental variables was measured in the field in each patch. Patch slope was measured using an Abney level and survey rod. Aspect of the patch was measured in degrees with a compass. We surveyed the distance to the channel and the height above the channel using the rod, level, and a distance meter. Patches were identified as either on terraces or depositional bars. The depositional bar is the lowest prominent feature higher than, but within, the channel bed, while terraces are older, higher fluvial landforms (Osterkamp and Hupp 1984). At every 0.5 m along the 50-m center line of each plot, we measured the intermediate axis of the surface particle at that point and assigned it to a size class, in a variation of the Wolman (1954) technique. Later, using Rodriguez's (1986) MOMENTS program, we calculated mean size, % < 1 mm, % < 2 mm, and sorting value for each patch. Soil samples of the upper 15 cm of the profile were taken in only 20 of the 67 patches, due to the cost of chemical analyses. These 20 samples spanned the spectrum of patch ages and floristic and environmental variation. Samples were later analyzed for standard fertility (organic matter, pH, N, P, and electrical conductivity) by the University of Wyoming Soil Testing Lab.

Quantitative Analyses

We used the SPSS/PC+ cluster analysis program (SPSS 1990) to determine groups of patches similar in overstory and understory vegetation composition (Romesburg 1984). After experimenting with several clustering methods, we identified the BAVERAGE method (average linkage between groups) and the cosine distance measure (angular separation of vectors of variables) as the best clustering combination. This combination emphasizes relative abundances within a plot and de-emphasizes absolute abundance differences between plots (SPSS 1990).

Species composition data were also ordinated by detrended correspondence analysis (DCA) using CANOCO (Canonical Community Ordination), a multivariate statistical program for applications in community ecology (Ter Braak 1988). Correspondence analysis provides a geometrical representation of the relationships among samples and species in a data set and identifies the dominant trend of variation in community composition.

Initial ordination and cluster analysis of the combined overstory and understory data set resulted in groupings primarily reflecting just the high cover values of overstory tree species rather than the joint pattern of both overstory and understory species. To counteract this, we analyzed the overstory tree species size-class data and the understory shrub and herbaceous species cover data separately, and then merged the two results. The overstory size-class data of each plot were first clustered; then the percent cover data of understory shrubby and

herbaceous species in each plot were clustered. These understory cover data were also ordinated using DCA. Final classification groups were the result of intersections of overstory cluster groups with understory cluster groups overlain on the understory DCA ordination diagram. We calculated the mean value for several environmental variables in each community type. Environmental variables we used are those found to be important to vegetational variation along the reach based on a separate, but related, gradient analysis (Baker and Walford 1995).

Classification groups referred to here are "community types" because they represent existing rather than potential natural vegetation. Each community type is based on the entire flora but is named based on the dominant species in the overstory and the dominant or most diagnostic indicator species in the understory (Mueller-Dombois and Ellenberg 1974). When there are co-dominants in a layer, both species are included in the name and are separated by a hyphen.

RESULTS

Classification

The cluster analysis and DCA ordination of the plot understory cover data (grasses, forbs, and shrubs) suggested four major groups and one outlier (Fig. 2). The similarity cut level was kept coarse so that overstory cluster groups could be incorporated later. This specific level was chosen after considering alternative cut levels at slightly greater or lesser similarity (Fig. 2). Groups A and B, for example, would become one group if the cut level were at a slightly lower similarity, yet these two groups are quite different (Fig. 2). Ordination of the same data set is represented by the DCA Axis 1 vs. Axis 2 ordination diagram (Fig. 3a). The distinctiveness of understory groups produced by cluster analysis is supported by the comparatively distinct location of the groups on this ordination diagram.

Understory groups identified by cluster analysis and ordination are compositionally distinct and occur in different environmental settings. Group A was dominated by *Alnus incana* and *Equisetum arvense*. These patches were predominantly located on bars. Group B was located entirely on bars and had the fewest species of any group. *Agrostis scabra* was always
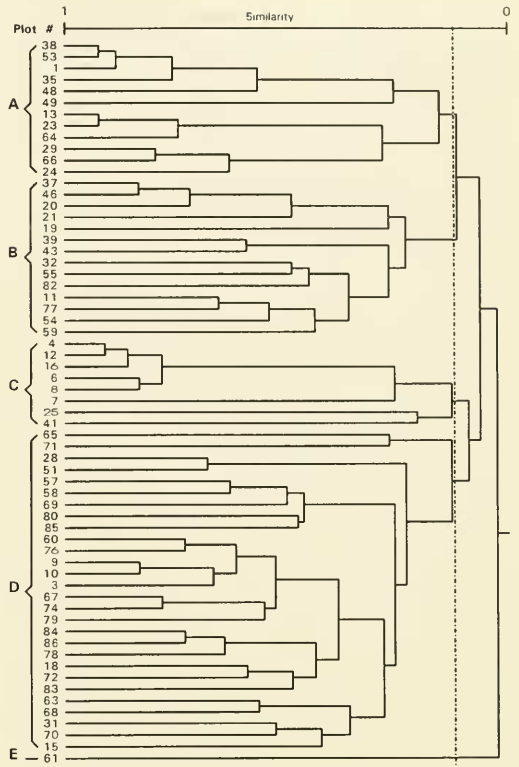
Fig. 2. Understory cluster analysis dendrogram based on percent cover of herbaceous and shrubby species. Plot numbers correspond with patch numbers on the study area map (see Fig. 1). The dashed line indicates the similarity level at which understory groups were separated.

present in Group B patches. The third group (C) was dominated by *Rosa woodsii* and *Pyrola asarifolia*. Patches of Group D are almost always on terraces and generally have the highest species richness. *Mahonia repens* is always present, and *Rosa woodsii*, *Bromus ciliatus*, and *Oryzopsis asperifolia* are usually well represented.

Overstory size-class data were clustered by the same method. Three overstory groups were identified at approximately 25% similarity (Fig. 4). Each of these major groups has members from at least three different understory groups. Group I is recognized by a dominance of *Populus angustifolia* seedlings, saplings, and small trees (Table 1). All understory Group B members are found within this overstory group. But other members of this overstory group have the understory of Groups A, C, D, or E. Overstory Group II is characterized by *Picea pungens* of all sizes and larger *P. angustifolia*

(Table 1). Most of its members have an understory of Groups A or D. The third overstory group tends to have a mixed canopy dominated by all sizes of *Pseudotsuga menziesii* and small *Abies concolor* (Table 1). *Populus tremuloides* and *Picea pungens* are often present. Half of the members of understory Groups C and D have this mixed overstory composition.

These overstory groups are indicated on the same DCA ordination diagram (Fig. 3b). Since this diagram represents the ordination of shrubby and herbaceous species in plots, and the understory composition varies within the overstory groups, it is not surprising that these overstory cluster groups are scattered within the ordination diagram. This suggests that the understory is to some extent independent of the overstory.

Final classification groups resulted from the intersection of the understory groups and overstory groups overlain on the ordination diagram (Fig. 3c). This results in eight final classification groups plus two single-member groups and one outlier plot. The symbol for each classification group is a combination of its overstory cluster group (I, II, or III; Fig. 4) and its understory cluster group (A, B, C, or D; Fig. 2). Groups are presented in an age sequence within their overstory group, from youngest (IB) to oldest (IIID).

Community Types

The following paragraphs summarize tree composition and structure, understory species composition, and environment of each of the eight community types (Tables 1, 2). In prior analyses (Baker and Walford 1995) the gradient controlling spatial variation of the shrubby and herbaceous vegetation mosaic was found to be age and disturbance related. Variables most affected by disturbance events are illustrated for each community type (Fig. 5). A map of the patches and their community type is in Figure 1.

[IB] *Populus angustifolia / Agrostis scabra.*— The 14 patches constituting this community type are found on bars close to the channel in both height and distance (Fig. 5). Of the eight major types, this type was most recently established (mean age = 31 years) and has the largest mean surficial sediment size. Its soils have low organic matter. Patches of this type are most common in the middle parts of the study reach (Fig. 1). This type is characterized by an abun-
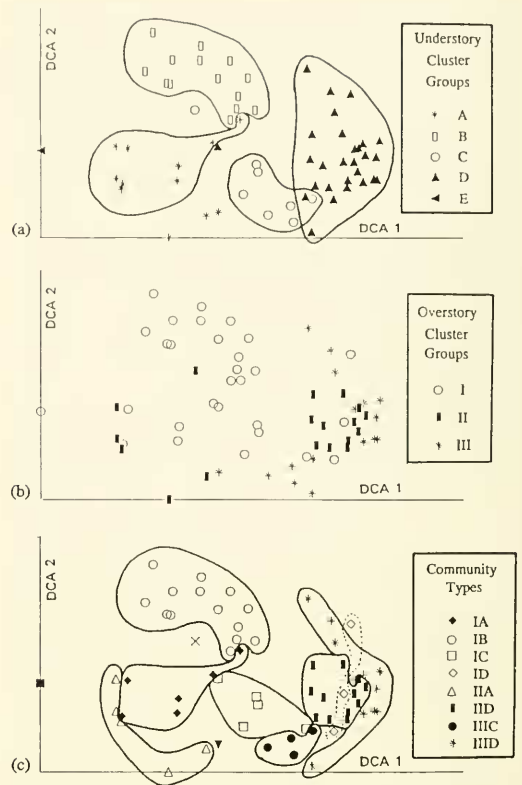
Fig. 3. Ordination diagrams obtained by detrended correspondence analysis of data on percent cover of shrubby and herbaceous species in the plots: (a) plots are coded according to their understory cluster analysis group (see Fig. 2); (b) plots are coded according to their overstory cluster analysis group (see Fig. 4); (c) plots are coded according to their final community type, based on the intersection of understory cluster groups with overstory cluster groups.

dance of *P. angustifolia* seedlings and saplings (Table 1) and sometimes small to medium-size trees. *Picea pungens* seedlings are almost always present and are sometimes abundant along with saplings and small trees. Small *Pseudotsuga menziesii* and *Abies concolor* may be present. Herbaceous vegetation is very sparse (Table 2). Graminoids dominate the understory with both *Agrostis scabra* and either *Trisetem montanum* or *T. spicatum* always present. *Epilobium latifolium* often occurs in significant amounts.

[IA] *Populus angustifolia / Alnus incana.*— Patches of this type are on average 10 years older than those of Type IB (Fig. 5). This community type is found on bars slightly higher above the channel than those of IB. Surface sediment sizes are diverse, but soils have little organic matter. Like Type IB, these patches
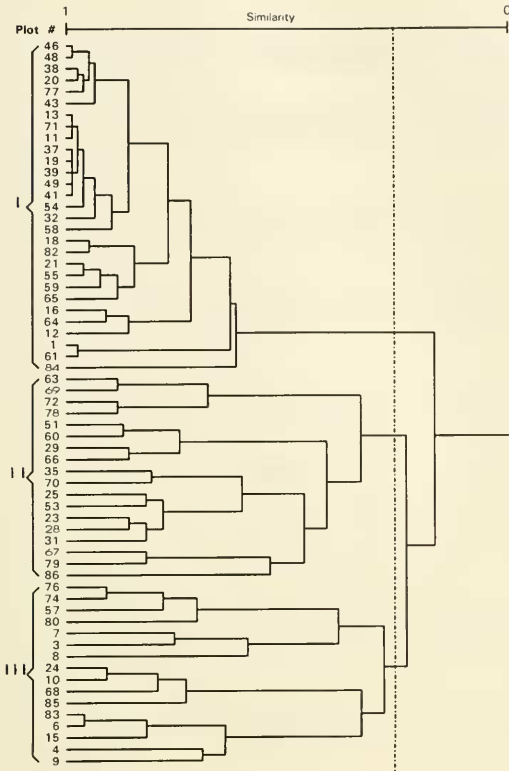
Fig. 4. Overstory cluster analysis dendrogram based on size-class data of tree species. Plot numbers correspond with patch numbers on the study area map (see Fig 1). The dashed line indicates the similarity level at which overstory groups were separated.

are most common in the middle part of the study reach (Fig. 1). *Populus angustifolia* characterizes stands of this type; many small and some medium-size trees are present along with abundant seedlings and saplings (Table 1). *Picea pungens* and *Pseudotsuga menziesii* seedlings and saplings are usually present. The understory composition distinguishes this type from IB (Table 2). Shrubs are more common. *Alnus incana* is always present and *Salix drummondiana* is usually present. *Agrostis scabra* is occasionally present in minor amounts.

[IC] *Populus angustifolia–Pseudotsuga menziesii / Pyrola asarifolia.*—This small community type comprises two patches on bars and one on a terrace, with an average surface particle size <10 mm and soils with low organic matter (Fig. 5). Patches in this community type are scattered along the study reach (Fig. 1). The largest trees and most abundant seedlings of this type are *P. angustifolia* (Table 1). *Pseudotsuga menziesii* are always present as seedlings

through medium-size trees. Medium-size *Picea pungens* or *Abies concolor* may also be present. *Pinus strobiformis* seedlings or saplings are always present in this type. The understory of this type is not dense, and all but one of the understory species have cover values <0.8% (Table 2). Three shrub species occur in small amounts. *Pyrola asarifolia* is always present in the highest amount of any understory species.

[ID] *Picea pungens–Populus angustifolia / Antennaria parvifolia.*—Three terrace patches and two patches on bars make up this community type, which occurs on surfaces <1 m above the channel that have soils with low organic matter content (Fig. 5). Patches in this type are scattered along the study reach (Fig. 1). They have strong similarities in overstory composition and weak ones in understory composition. *Picea pungens* and *P. angustifolia* are the largest trees of this type and are always present as seedlings, saplings, and small trees (Table 1). *Abies concolor* and *Pseudotsuga menziesii* seedlings can always be found. The lack of a constant understory is reflected in the low similarity level at which patches 65 and 71 are joined in the dendrogram (Fig. 2). Six species are present at 80% constancy, *Antennaria parvifolia* having the greatest mean cover in the type. No single herbaceous or shrubby species is present in all five patches of this type, but in general there is much more herbaceous and shrubby vegetation present than in types IA, IB, and IC (Table 2).

[IIA] *Picea pungens / Alnus incana / Equisetum arvense.*—Patches of this community type occur in more persistently moist areas. They span several age classes, can be found on bars or terraces, and have developed finer surficial sediments than might be expected for their age class (Fig. 5). Their soils typically contain only a little more organic matter than soils in patches of Type I. Patches in this type are scattered along the study reach (Fig. 1). *Picea pungens* seedlings, saplings, and small to medium-size trees as well as *P. angustifolia* of various sizes characterize the type (Table 1). Few other tree species occur, although *Pseudotsuga menziesii* may be present in small amounts. *Alnus incana* and *Salix drummondiana* are the dominant shrubs of this type, both occurring in greater amounts here than in any other types (Table 2). *Equisetum arvense* is always present in substantial amounts. Sedges

TABLE 1. Mean overstory stem density (no. stems per 0.1 ha) and percent constancy by species and size class within community types.

	Community type															
	IB		IA		IC		ID		IIA		IID		IIIC		IIID	
	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.																
seedling	4.6	50	7.5	33	1.0	33	17.6	100	2.0	20	11.8	83	162.0	75	77.5	100
sapling	1.7	14	0.8	33	0.7	33	3.0	80	1.2	20	5.6	67	32.0	50	11.5	91
3–13 cm	0.1	7	0.0	0	0.0	0	5.6	40	0.0	0	7.1	67	44.0	50	9.1	73
13–23 cm	0.0	0	0.0	0	0.0	0	4.6	80	0.4	20	2.4	50	10.0	75	3.0	55
23–33 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.8	25	4.0	75	1.5	36
33–43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.2	8	4.3	50	0.8	27
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.4	20	0.6	17	6.0	50	0.6	18
Picea pungens Engelm.																
seedling	37.9	86	25.7	67	7.0	67	42.8	100	91.6	100	19.0	100	4.8	50	11.6	73
sapling	8.1	64	7.5	50	1.3	67	14.2	100	44.2	100	13.3	92	0.3	25	4.1	82
3–13 cm	8.1	50	5.7	50	1.3	67	21.0	100	27.4	100	27.7	100	2.3	50	2.3	55
13–23 cm	0.6	21	1.0	33	1.3	67	5.8	80	9.6	60	9.2	83	0.3	25	1.8	55
23–33 cm	0.0	0	0.0	0	1.7	33	4.4	60	2.4	40	3.3	75	0.3	25	0.4	18
33–43 cm	0.0	0	0.0	0	0.0	0	3.0	60	0.0	0	1.8	50	0.3	25	1.1	36
>43 cm	0.0	0	0.0	0	0.0	0	2.2	40	0.4	20	1.3	42	0.0	0	0.5	27
Pinus ponderosa Laws.																
seedling	1.7	36	0.0	0	1.7	33	0.0	0	0.0	0	0.0	0	0.3	25	0.2	9
sapling	0.0	0	0.2	17	0.0	0	0.0	0	0.0	0	0.0	0	0.3	25	0.1	9
3–13 cm	0.2	14	0.7	17	2.0	33	0.0	0	0.0	0	0.4	17	0.5	25	0.0	0
13–23 cm	0.0	0	0.7	17	2.3	33	0.4	20	0.0	0	0.6	17	0.3	25	0.1	9
23–33 cm	0.0	0	0.3	17	0.3	33	0.2	20	0.0	0	0.2	8	0.0	0	0.2	18
33–43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	9
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	9

TABLE 1. Continued.

	Community type															
	IB		IA		IC		ID		IIA		IID		IIIC		IIID	
	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %	Stem #	Const %
Populus angustifolia James																
seedling	175.1	100	251.0	100	67.3	100	184.8	100	20.4	60	5.2	50	2.8	50	0.5	18
sapling	48.5	100	72.7	100	12.7	67	13.0	100	19.0	60	5.7	50	4.0	50	0.5	27
3–13 cm	20.5	79	51.2	100	14.7	100	14.4	60	7.8	60	7.8	67	3.8	50	1.8	27
13–23 cm	6.6	43	7.0	83	7.3	100	7.0	60	6.6	60	6.3	75	3.8	100	7.5	45
23–33 cm	1.5	14	1.8	33	7.0	100	3.6	60	5.0	60	7.1	58	7.5	100	5.6	36
33–43 cm	0.1	7	0.0	0	2.7	67	4.6	40	2.2	80	4.1	58	3.8	75	3.2	36
>43 cm	0.0	0	0.0	0	2.7	67	4.4	40	2.0	20	2.0	25	5.0	75	1.4	18
Populus tremuloides Michx.																
seedling	1.4	21	0.0	0	2.0	67	3.4	40	0.2	20	10.9	83	9.3	50	28.8	73
sapling	0.1	7	0.0	0	2.3	67	1.0	40	0.0	0	24.1	83	2.8	50	5.6	82
3–13 cm	0.0	0	0.0	0	0.0	0	4.0	40	0.0	0	8.8	92	0.3	25	10.1	100
13–23 cm	0.0	0	0.0	0	0.0	0	4.4	40	0.0	0	6.3	75	7.0	25	21.2	91
23–33 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	1.8	42	2.8	50	7.2	73
33–43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.8	25	1.3	50	0.6	36
>43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.1	8	0.0	0	0.2	9
Pseudotsuga menziesii (Mirbel) Franco																
seedling	9.5	86	30.8	67	18.0	100	13.6	100	2.4	80	7.4	83	21.0	100	26.0	82
sapling	2.4	50	4.8	33	4.0	100	4.6	80	2.8	60	6.1	75	12.0	100	12.0	91
3–13 cm	1.9	36	5.2	33	7.7	100	12.0	80	4.4	60	4.8	75	22.3	100	12.6	91
13–23 cm	0.0	0	3.2	33	5.0	100	4.0	40	1.6	20	0.9	33	15.8	100	3.5	64
23–33 cm	0.0	0	0.3	17	3.0	100	2.6	40	1.2	40	0.5	25	7.8	75	2.0	27
33–43 cm	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.3	17	1.0	50	2.3	64
>43 cm	0.0	0	0.0	0	0.0	0	0.6	20	0.0	0	0.1	8	1.3	50	0.5	36

TABLE 2. Mean percent cover values for main species in community types (includes species with at least 1% cover in any plot). Species with double underlined cover values had 100% constancy in that community type. Species with single underlined cover values had >80% and <100% constancy in that community type.

	Community type							
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
SHRUBS								
Acer glabrum Torr.	—	—	—	1.7	—	0.2	3.6	1.0
Alnus incana (L.) Moench ssp.								
tenuifolia (Nutt.) Breitung	0.1	0.8	—	0.1	5.0	—	5.1	—
Amelanchier alnifolia (Nutt.) Nutt.	—	—	0.1	0.6	—	0.6	1.0	1.2
Cornus sericea L.	—	—	—	—	—	—	2.4	—
Juniperus communis L.	—	—	0.1	2.3	—	3.9	0.4	2.7
Lonicera involucrata (Richars.)								
Banks ex Spreng.	—	—	0.1	0.1	0.1	0.4	0.2	—
Mahonia repens (Lindl.) G. Don	—	—	—	1.3	—	4.0	0.3	3.5
Prunus virginiana L.	—	—	—	—	—	1.6	1.4	0.5
Rosa woodsii Lindl.	—	—	0.1	2.1	—	1.8	1.5	3.1
Rubus parviflorus Nutt.	—	0.1	—	—	—	—	0.8	—
Rubus strigosus Michx.	—	—	—	0.4	0.1	0.2	0.4	0.5
Salix drummondiana Barratt								
ex Hook.	0.1	0.8	—	—	11.3	—	—	—
Salix lasiandra Benth.	—	0.4	—	—	—	—	—	—
FORBS								
Achillea millefolium L. var.								
lanulosa (Nutt.) Piper	—	0.2	—	0.9	0.1	1.0	—	0.8
Anaphalis margaritaceae (L.) Benth.								
& Hook. f. ex C. B. Clarke	—	—	—	—	0.3	0.1	0.1	—
Antennaria parvifolia Nutt.	—	—	0.1	2.9	—	1.2	—	4.0
Apocynum androsaemifolium L.	—	—	—	0.1	—	—	—	1.8
Arabis divaricarpa A. Nels.	0.1	—	0.3	—	—	—	—	—
Arabis hirsuta (L.) Scop.	0.1	—	—	—	—	—	—	—
Arctostaphylos uva-ursi (L.) Spreng.	—	—	—	—	0.1	—	0.9	0.2
Arnica cordifolia Hook.	—	—	—	—	—	—	0.7	—
Artemisia carruthii Wood ex								
Carruthers	—	—	—	0.3	—	—	—	0.1
Artemisia franserioides Greene	—	—	—	1.4	—	1.8	1.3	4.5
Artemisia ludoviciana Nutt.	—	—	—	0.8	—	0.1	—	0.2
Cerastium fontanum Baumg.	—	—	—	—	0.3	0.2	—	0.3
Epilobium angustifolium L.	—	—	0.3	0.3	0.1	0.5	0.2	0.3
Epilobium latifolium L.	0.7	0.1	—	—	—	—	—	—
Equisetum arvense L.	0.1	0.1	—	—	16.8	—	0.4	0.1
Erigeron eximius Greene	—	—	—	0.3	—	1.3	—	4.5
Erigeron flagellaris Gray	—	—	—	0.2	—	0.5	—	0.5
Erigeron formosisimus Greene	—	—	—	3.0	—	1.3	—	2.4
Erigeron speciosus (Lindl.) DC.								
var. speciosus	—	—	—	—	—	0.1	1.8	—

TABLE 2. Continued.

				Community type				
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
Fragaria vesca L. ssp. americana (Porter) Staudt	—	—	—	0.8	—	1.5	0.1	0.9
Fragaria virginiana Duchesne	—	—	—	0.3	—	0.6	—	1.4
Galium triflorum Michx.	—	—	0.1	0.7	0.1	0.2	2.6	0.6
Geranium richardsonii Fisch. & Trauty.	—	—	—	2.0	0.1	2.2	2.4	3.4
Haplopappus parryi Gray	—	—	—	2.4	—	2.1	1.5	1.5
Heracleum lanatum Michx.	—	—	—	1.0	—	0.2	2.2	3.6
Humulus lupulus L. var. lupuloides E. Small	—	—	—	—	—	—	—	0.1
Lathyrus brachycalyx Rydb.	—	—	—	—	—	—	—	0.3
Ligusticum porteri Coult. & Rose	—	—	—	—	—	—	0.7	0.1
Lithospermum multiflorum Torr. ex Gray	—	—	—	0.7	—	0.4	0.1	1.3
Mertensia franciscana Heller	—	—	—	0.2	—	0.2	1.1	0.9
Orthilia secunda (L.) House	—	—	0.1	—	—	0.1	1.1	0.2
Osmorhiza chilensis Hook. & Arn.	—	—	—	—	—	—	3.2	0.1
Osmorhiza depauperata Phil.	—	—	—	1.2	—	0.1	1.6	0.5
Oxytropis deflexa (Pallas) DC. var. sericea Torr. & Gray	—	—	—	1.3	—	0.1	—	0.2
Platanthera hyperborea (L.) Lindl. var. hyperborea	—	—	—	—	0.4	—	—	—
Potentilla hippiana Lehm.	—	—	—	1.0	—	0.3	—	0.8
Pseudocymopterus montanus (Gray) Coult. & Rose	—	0.1	—	1.4	—	0.6	0.1	0.4
Pteridium aquilinum (L.) Kuhn	—	—	—	—	—	—	—	0.1
Pyrola asarifolia Michx.	—	—	2.0	0.4	0.5	0.6	18.3	0.4
Rudbeckia laciniata L.	—	—	—	—	—	0.3	4.0	1.6
Senecio fendleri Gray	0.2	—	0.1	0.3	0.1	0.2	0.4	0.3
Silene menziesii Hook.	0.1	0.1	0.1	0.2	0.3	0.4	0.3	0.2
Smilacina stellata (L.) Desf.	—	—	0.1	5.1	—	3.8	1.7	2.3
Solidago canadensis L. var. salebrosa (Piper) M. E. Jones	—	—	0.1	0.1	—	0.1	0.1	0.2
Thalictrum fendleri Engelm. ex Gray	—	—	—	1.1	—	5.1	0.3	4.8
Thlaspi montanum L.	0.1	0.1	0.1	—	0.1	—	—	—
Urtica dioica L.	—	—	—	—	—	—	—	0.2
Vicia americana Muhl. ex Willd.	—	—	—	0.2	—	0.5	0.1	1.0
Viola canadensis L.	—	—	—	0.3	—	0.6	2.1	0.7
Viola nephrophylla Greene	—	—	—	—	—	0.3	0.1	—
GRAMINOIDS								
Agropyron trachycaulum (Link) Malte ex H.F. Lewis var. trachycaulum	—	—	—	—	—	0.4	—	0.2
Agropyron trachycaulum (Link) Malte ex H.F. Lewis var. unilaterale (Vasey) Malte	—	—	—	0.1	—	—	—	0.4

TABLE 2. Continued.

	Community type							
	IB	IA	IC	ID	IIA	IID	IIIC	IIID
Agrostis scabra Willd.	0.3	0.1	0.1	—	1.8	—	0.1	—
Agrostis stolonifera L. var. *stolonifera*	—	—	—	—	0.9	—	—	—
Blepharoneuron tricholepis (Torr.) Nash	—	—	—	1.2	—	—	—	0.4
Bromus anomalus Rurp. ex Fourn.	—	—	—	—	—	—	—	0.2
Bromus ciliatus L.	—	—	0.1	1.7	—	1.6	1.1	4.0
Calamagrostis canadensis (Michx.) Beauv.	—	—	0.2	—	0.1	1.3	0.6	0.7
Carex foenea Willd.	—	—	—	1.1	—	3.3	0.8	2.0
Carex kelloggii W. Boott ex S. Wats.	—	—	—	—	3.6	—	—	—
Carex pityophila Mackenzie	—	—	—	0.3	0.2	0.2	0.1	0.1
Carex rossii Boott ex Hook.	0.1	—	0.3	0.6	0.1	—	—	0.3
Deschampsia cespitosa (L.) Beauv.	0.5	0.1	—	—	1.1	—	—	—
Elymus glaucus Buckl.	—	—	—	—	—	0.1	0.4	0.6
Festuca thurberi Vasey	—	—	—	—	—	—	—	0.3
Juncus balticus Willd.	—	—	—	—	7.2	—	—	0.3
Juncus saximontanus A. Nels.	—	—	—	—	1.0	—	—	—
Juncus tenuis Willd. var. *uniflorus* (Farw.) Farw.	—	—	—	0.5	—	—	—	—
Koeleria cristata (L.) Pers.	—	—	—	—	—	0.1	—	0.6
Muhlenbergia richardsonis (Trin.) Rydb.	—	—	—	—	—	—	—	0.1
Oryzopsis asperifolia Michx.	0.1	—	—	1.3	—	1.7	3.6	6.2
Poa palustris L.	0.1	0.1	—	—	2.3	0.1	0.1	0.2
Schizachne purpurascens (Torr.) Swallen	—	—	—	—	—	0.2	—	0.1
Sitanion hystrix (Nutt.) J. G. Sm.	—	—	—	0.1	—	0.1	—	0.6
Stipa columbiana Macoun	—	—	—	—	—	0.1	—	0.2
Trisetum montanum Vasey	0.4	0.1	0.1	—	0.8	—	—	—
Trisetum spicatum (L.) Richter	0.1	—	0.1	0.1	—	—	—	—
EXOTICS								
Poa pratensis L.	0.8	—	—	1.2	—	2.8	0.1	3.7
Poa trivialis L.	—	—	—	—	2.3	—	—	—
Taraxacum officinale Weber	0.1	0.1	—	0.6	0.1	1.4	0.1	0.5

and rushes dominate the graminoid layer, with *Juncus balticus* always present.

[IID] *Picea pungens–Populus tremuloides / Mahonia repens.*—Ages of these patches span the range from 40 to 130 years. Most are found on terraces, with 89% of their surficial sediment <1 mm in size (Fig. 5). Soils in this type contain moderate amounts of organic matter (Fig. 5). Patches in this community type are most common in the upper two-thirds of the study reach (Fig. 1). This type is characterized by *P. tremuloides* and *P. pungens* of all sizes (Table 1). *Populus angustifolia* is not regenerat-

ing strongly but is sometimes the largest tree in a patch. *Abies concolor* and *Pseudotsuga menziesii* may also be present, usually in small sizes. *Mahonia repens, Juniperus communis,* and *Rosa woodsii* are dominant shrubs (Table 2); *Thalictrum fendleri* and *Smilacina stellata* are dominant forbs. The graminoid layer is characterized by *Bromus ciliatus*, with significant amounts of *Carex foenea* often present.

[IIIC] *Pseudotsuga menziesii / Acer glabrum / Pyrola asarifolia.*—The four patches of this community type are all found on terraces with fine surface sediments, have about the same
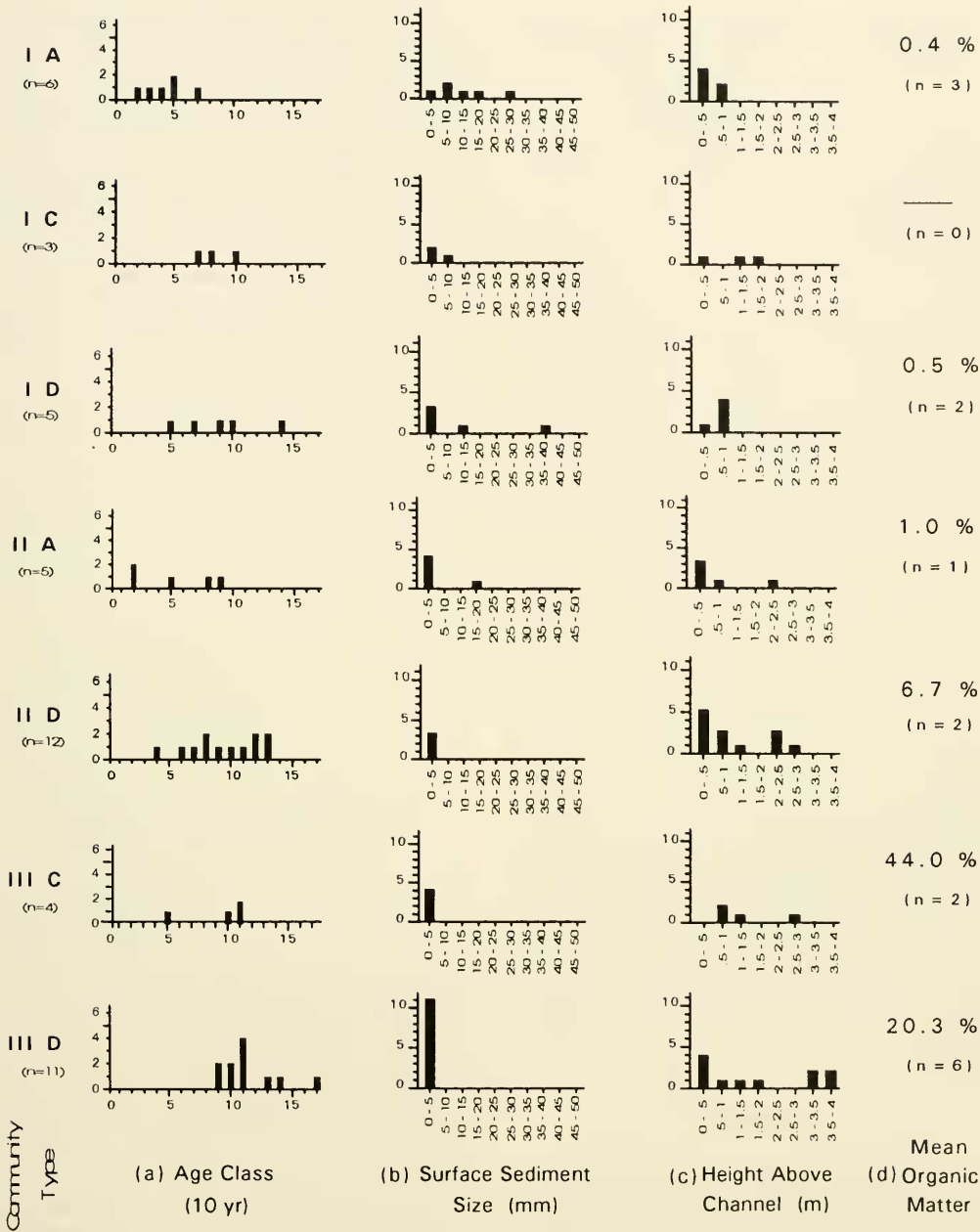
Fig. 5. Environmental attributes within each community type (see Fig. 1). Histograms (a–c) show the frequency on the vertical axis.

age-class span as patches in Type IID, and have the largest mean organic matter content of community types along the reach (Fig. 5). The overstory is a mixed forest similar to Type IIID, but the understory is not as rich. Patches in this type are restricted to the lower one-third of the study reach (Fig. 1). *Pseudotsuga*

menziesii, *Populus angustifolia*, and usually *Abies concolor* are the large trees of these patches (Table 1). *Populus angustifolia* seedlings or saplings are rare. Regeneration appears strongest in *Abies concolor* and *P. menziesii* (Table 1). *Acer glabrum* is the dominant shrub usually associated with lesser amounts of *Alnus*

incana, *Prunus virginiana*, and *Rosa woodsii* (Table 2). *Pyrola asarifolia* is the most prevalent forb with cover values averaging 18%. *Geranium richardsonii*, *Smilacina stellata*, *Haplopappus parryi*, and *Artemisia franserioides* always occur. *Oryzopsis asperifolia* is the dominant graminoid, with *Bromus ciliatus* in lesser amounts.

[IIID] *Populus tremuloides–Pseudotsuga menziesii / Bromus ciliatus.*—Examples of this community type are found on terraces an average of 1.75 m above the channel (Fig. 5). Surface particles are predominantly <1 mm, while soils have about 20% organic matter content (Fig. 5). The 11 patches comprising this type have the oldest average age and are most common in the lower one-third and upper one-third of the study reach (Fig. 1). This group of patches is a mixed forest type, with the densest understory of all the types. *Populus tremuloides* and *P. menziesii* tend to be the largest and the most abundant trees of these patches. Some patches have very large *Populus angustifolia* as well. *Abies concolor* seedlings and saplings are always present, sometimes in very large numbers. A few *Picea pungens* of various sizes usually can be found. *Mahonia repens*, *Rosa woodsii*, and *Juniperus communis* are co-dominant shrubs. Five *Erigeron* species were found in the 11 patches of this type, with one to three species present in each patch. *Antennaria parvifolia* and *Geranium richardsonii* had high cover values in most patches. Dominant grasses were *Bromus ciliatus* and *Oryzopsis asperifolia*, their quantities being distinctive from any other type.

DISCUSSION

The New Classification Technique

Ecologists working in northern climates have long recognized that individual stratal layers (e.g., tree and shrub) or "synusia" within forest communities may be distributed somewhat independently and may not all have the same value in distinguishing vegetation units (Whittaker 1962). Classification approaches of the northern European schools, such as the "sociations" of the Uppsala school and "sitetypes" of Cajander (Whittaker 1962), emphasize that lower strata often are more useful in classification, although the tree layer is of some importance as well.

Yet, common multivariate techniques for analyzing vegetation data ignore the synusial affiliations of the species in a community (e.g., Gauch 1982). Since cover values of overstory tree species are often large relative to cover values of understory species, overstory species may prevent understory species from having much influence on the outcome of multivariate analyses (e.g., Padgett et al. 1989). Moreover, these techniques do not take advantage of the different kinds of data that are useful in describing the structure of different synusia. For example, it is much easier and more useful to obtain size-class structure data than cover data for overstory trees in forests, as size-class data can indicate tree composition and abundance as well as population structure (e.g., regeneration status). The value of both kinds of data in forests has long been recognized (e.g., Pfister et al. 1977). Yet, size-class data and cover data are incompatible and cannot both be used readily in a single multivariate analysis. The technique used here allows an equal consideration of both the understory and overstory data and data of different types from different synusia. Community types that are produced have homogeneous tree populations combined with homogeneous understories.

Community types identified using this technique can be useful in conservation and management. The eight community types reflect major variations in vegetation and environment along the reach. A preserve could be designed, shorter than the full length of the reach, that contained all eight community types; it is likely that much of the floristic variation along the reach would then be protected. Moreover, the community types should be useful in management because they are (1) functionally homogeneous, in the sense that tree populations within a type might respond similarly to disturbances, and (2) environmentally sensitive, in the sense that the finer environmental discrimination of understory synusia common in northern regions has been incorporated.

The Community Types in a Regional Context

Community types identified in this study have not been widely reported. This is probably due to the river-reach scale of the study and the tendency to exclude very young vegetation in developing regional classifications. This is also one of a very few river systems in the

southern Rocky Mountains with a complete mosaic of riparian vegetation relatively free from human land uses; thus, there have been few other opportunities for this kind of study.

Our Type IIIC is very similar to Baker's (1989) *Abies concolor–Picea pungens–Populus angustifolia / Acer glabrum* association, previously found along the Animas River and the San Juan River, as well as in northern New Mexico (DeVelice et al. 1986). Baker collected data from within the study reach, which explains the similarity of his association with our Type IIIC, but his goal was to classify vegetation regionally based upon the similarity of the more mature vegetation patches along separate rivers. Baker did not sample the mature stands containing *Populus tremuloides* that are found in our Type IID and IIID, thinking they were earlier successional stages of our Type IIIC. However, the age-class data (Fig. 5) suggest that stands within Types IID and IIID are just as old as or older than those in Type IIIC. Thus, although it may be a necessary shortcut for regional classification efforts, sampling and classifying only the mature vegetation may result in errors if the successional sequence along a reach is not clearly understood.

Sampling and Classification of Riparian Vegetation Complexes

In riparian areas, and perhaps anywhere vegetation classification is being approached, it is important to sample and classify not only mature vegetation stands but younger stands as well. The diverse patch structure along rivers may only reach a homogeneous mature composition similar to that in the older patches if the fluvial disturbances that have produced the mosaic are controlled. Moreover, younger stands may not all be leading to the same mature community; there may instead be more than one seral sequence.

This spatial and temporal complexity at the river-reach scale compounds the difficulty of developing regional classifications. One solution to this problem is to adjust the scale of sampling to the scale of patchiness produced by the primary ecological processes (e.g., fires, floods) in a particular landscape. An area such as this free-flowing river requires fine-scale sampling as there is a fine-scale mosaic produced by disturbances and geomorphic variation. A river with less geomorphic complexity or a coarser, more infrequent flood-produced

patchiness may require only a coarse sampling focused on the more mature vegetation.

Spatial Variation in Vegetation Along the Reach

The sampling and vegetation analysis suggest that substantial landscape diversity is produced by floods and geomorphic variation along this reach of the Animas River (Fig. 1). The spatial arrangement of this diversity is controlled in part by location of tributaries and width of the valley floor, both of which influence how and where floods create new patches. Needle Creek flows into the Animas River in approximately the middle of the study reach (Fig. 1). Smaller tributaries enter above and below this point, but none carries as great a volume of water. The valley floor also widens approximately 0.5 km below the entry of Needle Creek.

The first four community types (IA, IB, IC, and ID) with *Populus angustifolia* in their overstory are found primarily in this section at the outer river curves or mid-channel where scouring is greatest. The wet environment IIA patches also are found in this wider section, often away from the main channel on side channels that dissect major patches. None of the largest trees is found in this middle section of the reach. In contrast, community types with a more mature overstory are more common in the lower one-third and upper one-third of the study reach. These parts are narrower and have fewer substantial tributaries. Many of the mature vegetation patches are located on terraces quite high above the channel in these parts of the reach.

Conclusions

This study of riparian vegetation on the river-reach scale revealed considerable spatial and temporal complexity. Flood disturbances, modulated by variation in valley morphology and tributary location, have created distinct patchiness in the vegetation. A new technique, based on both overstory and understory species, offers an improved quantitative method for identifying community types. If classification is to be used effectively to aid in conservation, greater attention to younger, less mature stands of vegetation may be needed. These young stands are a major component of the biodiversity on the river-reach scale and can represent

seral stages of new vegetation associations unlike the association represented by present mature stands. Spatial complexity along a single river may make the development of regional classifications, based on many rivers, more difficult. However, regional classifications can still be completed, and will be more valuable, if sampling efforts are tuned to the scale of patchiness and complexity along river reaches.

ACKNOWLEDGMENTS

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